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Vertebrate remains from a stratified Holocene deposit in Skull Cave, Western Australia, and a review of their significance

by J. K. Porter

9 Violet Grove, Shenton Park, W.A. 6008

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Abstract

Skull Cave is a collapse doline which has acted as a pit trap to animals living in the vicinity of the cave. A small excavation was made in a richly fossiliferous sandy floor deposit and 22 species of mammals were recorded. Comparisons are made with other modern and fossil records from this region and it is suggested that a retraction northwards or local extinction of three taxa *(Bettongia lesueur, Petrogale* sp. and *Notomys* sp.*)* occurred during early Holocene time and of two taxa *(Perameles* sp. and *Pseudomys albocinereus)* at some time after 3 000 years B. P. but before historic time. Evidence for the invasion of this region by another species *(Rattus tunneyi)* about 3 000 years ago was found. All of these taxa are known to inhabit heath or scrubland but not forest. During the Holocene, there appears to be a considerable degree of stability in the composition of fauna which include forest in their habitat. Human remains and some artifacts were found, but it is questionable whether the cave was an occupation site. Two radiocarbon dates based on charcoal indicate that the deposit so far excavated spans most, if not all, of Holocene time.

Introduction

Skull Cave is situated in aeolian Tamala Limestone of the Cape Leeuwin-Cape Naturaliste region, at latitude 34° 17′ south and longitude 115° 06′ east (Fig. 1). It is registered with the Lands and Surveys Department as cave AU 8 (Bridge 1973).

The cave comprises a large main chamber with a partially collapsed roof forming the entrance, and a small extension leading off the western part of the chamber. A large rubble pile about 13 m in height from the present sandy cave floor has formed below the entrance. The cave walls are either overhanging or nearly vertical, and there is a further 10 m approximately from the top of the rubble pile to the entrance above, hence the cave now acts as a pit trap to many of the animals living in its surroundings. Both chambers have been partially filled with sandy sediments washed into the cave, and the excavation walls show thin interfingering bands of brown, orange and sometimes whitish coloured sediments. Much charcoal is present throughout the deposit.

Remnants of a breccia were noticed adhering to the cave wall about 2.5 m to 3 m down from the entrance. Examination of the samples (G13407) collected suggest that this sediment is part of a previous cave floor which has since collapsed into the main chamber below. No biotic remains were found in any of the breccia collected.

Skull Cave is located in one of the several patches of open forest in this area and is surrounded by high closed forest of *Eucalyptus diversicolor* to the east and north, open scrub (the principal component being *Agonis flexuosa*) merging into low open scrub to the west and low open woodland (*A. flexuosa*) to the south (Smith 1973). Further north and east is open forest principally of *E. marginata*.

The excavation and methods

During November 1969, a small excavation was begun in the southern part of the main chamber (see Fig. 2) and was completed in 1971. The trench, later recorded as Trench A, was 1 m wide and 1.5 m long and it was excavated to a depth of 190 cm where a thick crystalline flowstone was encountered. In March 1973, a second trench (Trench B) was begun adjacent to Trench A; its dimensions were 1 m wide and about 1 m long, and about 115 cm deep. At this depth the sediment was so firmly cemented by calcium carbonate that excavation even with hammer and chisels was ineffective. This trench was completed in 1975.

Because the different layers or bands in the deposit were usually less than 1 cm in thickness, excavation by natural stratigraphic layers was not feasible and was therefore done by arbitrary levels, following the general dip of the sediment. All depths were measured from the sandy floor surface.

Figure 1.—Location of fossil sites in the Cape Leeuwin-Cape Naturaliste region, Western Australia.

Material excavated from both trenches was shaken on a sieve of 3 mm square openings and all bone was retained. Stone material of artifactual or geological significance was also kept. All specimens are lodged at the Western Australian Museum.

Accumulation and nature of the bone sample

The structure of Skull Cave renders it an efficient pit trap to animals living in the area, and it is likely that much of the faunal sample accumulated in this way. In fact two animals, a Pigmy Possum *(Cercartetus concinnus)* found on the surface in "shallow excavation" (see Fig. 2) and a domestic cat found near the base of the rubble pile, fell into the cave during the period of my visits. Accumulation of bone in a similar manner has been previously described in Australia (e.g. Bain 1962, Lowry and Lowry 1967) and elsewhere (e.g. Martin *et al.* 1977).

Within the deposit excavated in Trenches A and B, bones were found often still articulated, and in several cases skull, dentaries and some post-cranial bones, all attributable to the same individual, were recovered. These associations of several bones of one animal indicate that little disturbance has occurred since the animal died or was deposited in that position. An excellent example of this was found in the lowest levels of Trench B where parts of the skeleton of an adult Grey Kangaroo *(Macropus fuliginosus)* were collected. The limb bones were still articulated but both tibiae were broken, presumably resulting from the animal's fall into the cave; the breaks were not fresh but thinly coated with calcium carbonate, and the two parts of each bone had not been displaced as might have been expected if they had been broken by a falling rock.

A small proportion of the bone sample may have been washed into the cave along with sediments from the surface outside or washed to the excavation site from the rubble pile. Mechanical abrasion and/or chemical weathering were noted on only two specimens (each a dentary fragment of *Pseudocheirus peregrinus* 76.10.291 and *Trichosurus vulpecula* 76.10.369) and it is possible that these specimens were derived from either the rubble pile or, more likely, outside the cave. Some specimens were possibly reworked from another locality within the cave; similar cases are discussed by Archer (1974) and Milham and Thompson (1976). While it is believed the bone sample from Trenches A and B was mostly *in situ*, evidence of possible reworking within the cave has been found; a calcaneum identified as *Zygomaturus* has been recovered from a depth of 265.5-365.5 cm in an excavation made by R. Howlett, (pers. comm.). *Zygomaturus* has been previously recorded from a Pleistocene deposit in Mammoth Cave and from Strongs Cave (Merrilees 1968) and a tentative identification of a single tooth as *Zygomaturus* has been made at Devil's Lair (Balme *et al.* 1978). All of these finds are from sites considerably older than the dated deposit excavated in Skull Cave. The breccia in Skull Cave may have been the original source of the *Zygomaturus* specimen, and its contemporaneity with the sediments from which it came is in some doubt.

Bones representing several taxa showed evidence of charring: *Antechinus flavipes* (76.10.55), *Isoodon obesulus* (76.1.99), *Perameles*

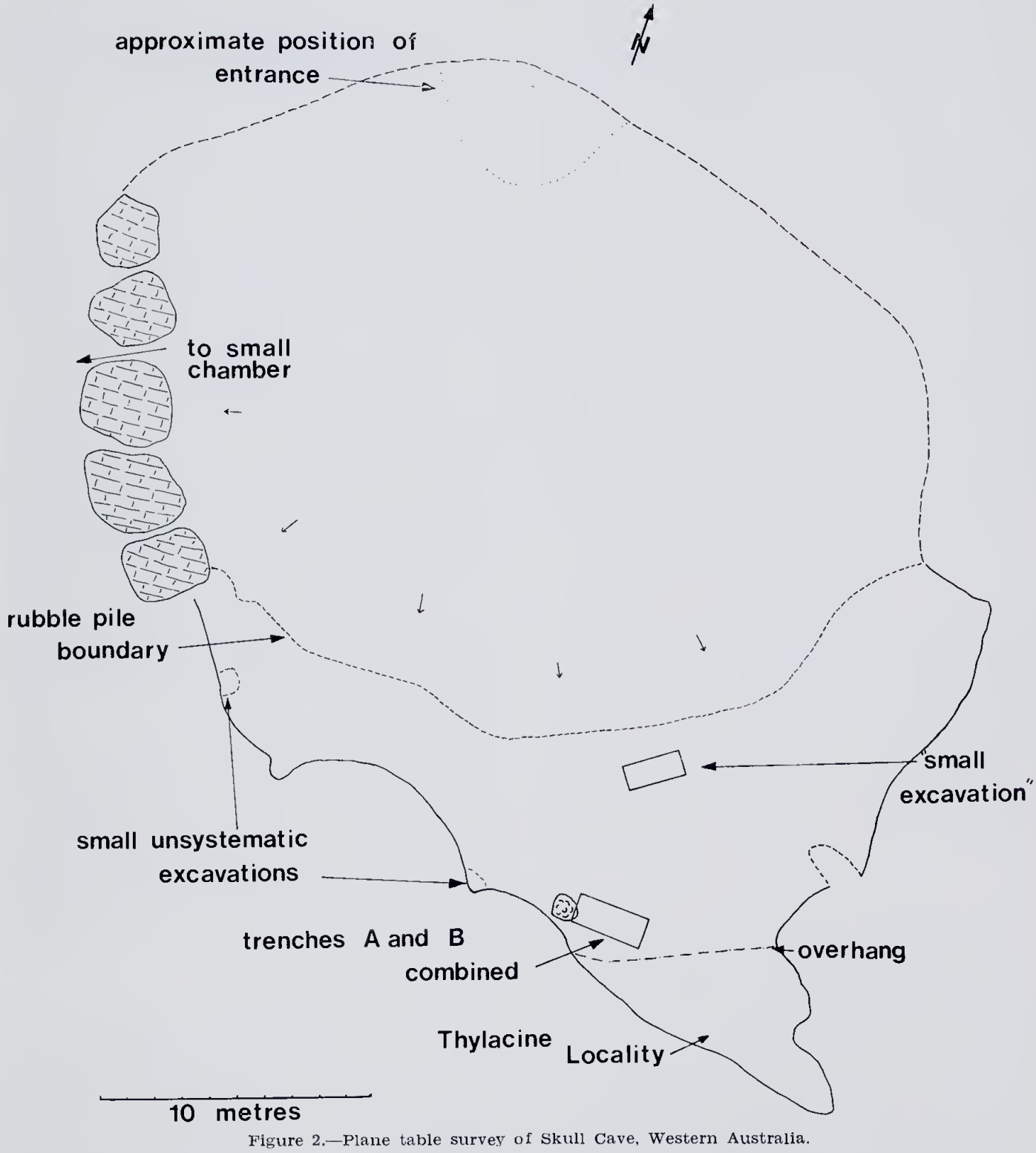

Figure 2.—Plane table survey of Skull Cave, Western Australia.

sp. (76.10.287), *Pseudocheirus peregrinus* (e.g. 76.10.244) *Potorous tridactylus* (76.1.119), *Setonix brachyurus* (e.g. 76.1.120) and *Rattus fuscipes* (e.g. 76.10.186). Charred bone occurring in caves could result from cooking or burning of animal carcases in hearths made by human occupants or could be the remains of animals charred during a bushfire and later washed into the cave. Several large charred tree trunks or limbs are present on the rubble pile in Skull Cave, and it is probable some charring of the many bones scattered over its surface occurred within the cave. While both artifacts and human remains (see below) have been recovered from various parts of the cave, they are few in number and no other evidence suggesting occupation of the cave has been found as yet. In its present state the cave would probably have been inaccessible to humans unless some structure was made to reach down from the

upper part of the cave wall to the top of the rubble pile. The possibility remains that the cave was used by humans but it is likely that such visits, if they occurred, were infrequent, and the few fragments of charred bone recovered were sparse and were probably charred by natural agencies.

Owls may have used the cave as a roost and the remains of smaller animals (especially murids and small dasyurids) from regurgitated pellets could have been incorporated into the deposit in this way. There is not a large preponderance of such smaller animals as is typical of owl-pellet deposits (Archer and Baynes 1972) and it is considered that owls were not major contributors to the faunal sample. However, even a small contribution may be of significance. Much of the bone sample resulted from animals falling into the cave by chance, and such a sample would be representative of at least part of the fauna living in the immediate cave surrounds. The presence of *Perameles*, *Pseudomys albocincreus*, *P. praeconis* and *P. shortridgei* (see below) which are known to inhabit heath and scrubland, but not forest may be due to owls which include both regions in their predatory range.

Age of the deposit

Two radiocarbon dates based on charcoal samples were obtained from an upper and intermediate level in the excavation. The upper level, 21-28 cm in Trench B, was dated as 2 900 ± 80 yr B. P. (SUA 227) and the intermediate level, 100-115 cm in Trench A, yielded a date of 7 875 ± 100 yrs B. P. (SUA 228).

A depth of 190 cm was reached in Trench A and assuming a constant rate of accumulation of sediments, this level can be roughly estimated as late Pleistocene or perhaps early Holocene.

The human components

The remains of more than one individual of *Homo sapiens* have been found in different parts of Skull Cave. A nearly complete mandible (A 22738) was discovered in the small western extension. It was found on a limestone boulder but was covered in brown dust typical of the cave sediment and was probably dug from the deposit nearby. No teeth are present in the mandible and the specimen was probably considered an uninteresting bone possibly from one of the several unsystematic "digs" in the cave. In Trench B, 28-34 cm, a human metatarsal (A 22915) was recovered, and a complete radius of an adult (A 22968) was found on the surface of the rubble pile.

A few artifacts of quartz, limestone and bone were excavated from Trenches A and B and are included in Table 1. Other small pieces of quartz, usually between 2 and 4 cm in diameter were also found, showing considerable rounding but no sharp fracture surfaces. These may have been the "cropstones" of birds. Tyne and Berger (1959) note that many seed-eating birds eat grit and Meinertzhagen (1954) mentions that quartz is often ingested. Six flaked quartz fragments may be remnants of flaking, presumably done on the forest floor outside the cave and subsequently washed in along with sediments. One quartz flake and two chips were also found.

A flaked bone splinter showing fracturing along one edge (presumably from use) was excavated from 115-127 cm in Trench A. The artifact was made from the limb bone of a large animal, probably a Grey Kangaroo, *Macropus fuliginosus*.

All archaeological specimens have been lodged in the Archaeology Department of the Western Australian Museum with the catalogue numbers B 2597, B 3517, B 3518, B 3523, B 5430-B 5439.

The fauna from trenches A and B

Trenches A and B were dug in arbitrary levels with depths measured from the cave floor surface; data from the two trenches were combined and are given in Table 1. Estimates of the minimum numbers of individuals were made using methods described by Baynes *et al.* (1976) and for names and species concepts I have followed Ride (1970). Catalogue numbers for the vertebrate fauna are 70.7.187-70.7.348, 71.10.115-196, 74.8.5-222, 76.10.1-438, 76.10.484-487.

Many land snails were recovered from the surface of the cave and within the excavated deposit, and these are lodged in the Palaeontology collection of the Western Australian Museum.

From about 115 cm to the bottom of each trench, sediments were cemented by calcium carbonate such that the whole of the bone sample from these levels was not easily retrievable, and numbers of individuals in these layers are notably fewer. Generally, numbers of individuals of most species recorded are too few to suggest trends or changes in relative abundance. However some emphasis can be placed on the presence or absence of certain species within the deposit as compared with other records for this region.

Comparison of the faunal assemblage with modern records

At the time of arrival of European man in Western Australia, the mammal fauna of the Cape Leeuwin-Cape Naturaliste region included *Dasyurus geoffroii*, *Phascogale tapoatafa*, *Sminthopsis murina*, *Trichosurus vulpecula*, *Pseudocheirus peregrinus*, *Cercartetus concinnus*, *Tarsipes spencerae*, *Bettongia penicillata*, *Macropus fuliginosus*, *Setonix brachyurus*, *Hydromys chrysogaster* and *Rattus fuscipes*, and it is probable that *Antechinus flavipes*, *Isoodon obesulus*, *Potorous tridactylus*, *Pseudomys praeconis*, *Pseudomys shortridgei*, *Rattus tunneyi* and *Canis familiaris* were also present (Baynes *et al.* 1976). *Sarcophilus harrisii* has not been recorded from this area during historic time. However, Archer and Baynes (1972) report a *Sarcophilus* tooth from a deposit dated

Table 1

Minimum numbers of individuals of mammals and other vertebrates excavated from Trenches A and B combined, and artifacts recovered.

Depth from surface	*Dasyurus geoffroii*	*Phascogale tapoatafa*	*Antechinus flavipes*	*Sminthopsis murina*	*Sarcophilus harrisii*	*Isoodon obesulus*	*Perameles* sp.	*Trichosurus vulpecula*	*Pseudocheirus peregrinus*	*Cercartetus concinnus*	*Tarsipes spencerae*	*Potorous tridactylus*	*Bettongia penicillata*	*Macropus fuliginosus*	*Setonix brachyurus*	*Hydromys chrysogaster*	*Pseudomys albocinereus*	*Pseudomys shortridgei*	*Pseudomys praeconis*	*Rattus fuscipes*	*Rattus tunneyi*	*Canis familiaris*	bats	birds	lizards	snakes	frogs	artifacts	C^{14} dates
cm																													
0– 7	....	1	3	3		5		3	3	2	....	2	1	1?	3	....	....	4	....	14	4	....	....	7	7	P	16	2 flaked quartz fragments 1 quartz chip	
7– 14	1	1	5	4	....	4	1	4	5	2	.	3		1	5	...	.	2	.	12	4	...	1	8	5	P	21	flaked calcrete fragment	
14– 21	2		3	.	....	3	...	4	5	2	....	4	2	1	6	....	....	3	....	6	4	1	. .	4	5	P	30	? flaked bone fragment	
21– 28	1	1	6	1		2		4	4	1	.	3		1	5	1	1	2		9	1	.		11	5	P	21	3 ? limestone artifacts	2 900 ± 80 yr B.P.
28– 35	.	.	2			1	1	2	1	1	..	1	....	1	3	....	....	1	....	7	....	....	....	5	1	P	6		
35– 42	....	....	3	...	1	2	1	1	5	3		2		1	3	...	2			5	....	..	1	9	6	P	28		
42– 63		1	10	2	. .	3	2	6	6	8	..	4	....	2	7	....	1	2	....	18	....	. .	....	8	12	P	87		
63– 70	2	....	10	1	....	2	1?	2	3	3		3	....	1	3	1	1	1	.	12	....	....		4	8	P	58	1 flaked quartz fragment	
70– 80	2	2	11	5		3	1?	5	4	11	1	1	....	1	4	....	3	3	1	27	....	....	....	7	12	P	39	1 quartz flake	
80– 90	1	1	4	5	....	2	1	1	4	17	....	1	....		4	. .	1	1	1	22	....	....	..	11	10	P	36		
90–100			4		....	1	1	2	6		.	..	....	..	3	....	....	1	....	5	....	....	....	6	3	P	16	flaked calcrete fragment	
100–115	1	1	7	2	....	2	1	2	4	11	....	1		2	3	....	. .	1	2	11	....	....	.	4	4	P	6	quartz chip	7 875 ± 100 yr B.P.
115–127		.	5	2	....	....	....	2	2	2	...	2	....	....	1	....	....	1	1	10	....	....	....	5	1	P	6	flaked quartz fragment bone splinter	
127–137			4	5	..	.	1	1	2	5	..	....		...	1	....	3	.	....	18	....	....	....	8	1	P	4		
137–144	....	1?	1	....	...	....	....	2	1	3	....	....	..	1	1	. .	3		...	3	....	....	...	2	3	P	1		
144–150			1	1?	....	....		1	1	2	..	..	....	1	1	....	..	2	....	4	....	....	....	2	1	P	1		
150–160	....	....	....	1	....	1	....	1	2	2	....	1	....	1	2	....	2	....	....	2	....	....	.	1	2	P	2	flaked quartz fragment	
160–170	....	....		1	...	....	. .	1	1	1	.	..	.	....	1	....	..	....	....	1	....	....	....	..	..	P	....	flaked quartz fragment	
170–180	....	....	....	....	....	....	....	1	1	1	....	1	....	....	....	....	....	....	....	1	....	....	..	1	.	P	....		
180–190	....	. ..	1	....	....	....	....	....	1	....	....	....	....	....	....	....	....	1	....	....	....	....	....	....	....	P	....		

P = present

430 ± 160 yr B. P. and in light of this date suggest the species may have been extant in this region at the time of European arrival.

All of these species occur in the Skull Cave deposit and a further two, *Perameles* sp. and *Pseudomys albocinereus,* were also recovered although they have not been recorded historically.

Comparison of the faunal assemblage with other fossil records

Only one fragment of *Sarcophilus harrisii* was recovered from Trenches A and B, but other specimens have been collected from within the cave. An interesting skull (71.10.209) with an aberrant tooth, which has been illustrated by Archer (1975), was collected by P. Kendrick in 1971 from the surface of a not easily accessible part of the cave floor where the cave wall is low. There is no reason to suspect that the specimen was not *in situ;* it is probably of quite recent age. Other records of *Sarcophilus* have also been made from several caves in this region (Lundelius 1960, Merrilees 1968, Baynes *et al.* 1976).

Pseudomys albocinereus has been recorded from various levels in Skull Cave, the youngest from a level 21-28 cm below surface which has been dated 2 900 ± 80 yr B. P. (SUA 227). Other sites from which this species has been found are Cave 3 at Turner Brook (Archer and Baynes 1972), Yallingup Cave from a deposit below two flowstones (Merrilees 1979), and at Devil's Lair (Baynes *et al.* 1976) (see Fig. 1).

Perameles has been recorded from Mammoth Cave in which it occurs more commonly than *Isoodon* (Merrilees 1968) and in Devil's Lair in which it is less abundant than *Isoodon* but not uncommon (Balme *et al.* 1978). Isolated specimens have also been found in Brides Cave, Cave Au 12 and Harleys Cave. Merrilees (1968) suggested that *Perameles* may have become extinct in this region in relatively recent time. The youngest specimen found in the Skull Cave deposit was at a depth of 7-14 cm below the surface. The specific identity of these various specimens has not yet been determined, but it has here been assumed they are conspecific.

The only record of *Tarsipes spencerae* from the Skull Cave excavations was from a level 75-80 cm depth in Trench A. Devil's Lair is the only other site in the Cape Leeuwin-Cape Naturaliste region where the species occurs as a fossil (Balme *et al.* 1978). Outside this region, the only other Western Australian fossil record is from Koala Cave near Yanchep (Archer 1972). The lack of records for this species is probably in part due to its fragility (Baynes *et al.* 1976), but it is also likely that cranial and mandibular remains, especially if broken, may easily pass unrecognised. Devil's Lair is the only site from which such specimens have been identified and these are mostly dentaries. In both Skull Cave and Koala Cave, and in most cases in Devil's Lair, identifications have been made on postcranial remains, commonly femur, humerus and pelvis,

Bettongia penicillata was present on the surface of Skull Cave and in the uppermost levels of Trenches A and B to a depth of 21 cm. There are several other records of this species for this region, both of considerable age (e.g. from Devil's Lair) and probably quite recent (e.g. from the surface of Harleys Cave). It is interesting to note that although *B. penicillata* was found on the surface in Harleys Cave, no specimens were recorded from the one metre of deposit excavated by R. Howlett. This absence from all but the uppermost levels in both of these caves may be a reflection of low population numbers during that time, or perhaps a contraction away from this area of the Cape Leeuwin-Cape Naturaliste region of the range of this species during the early part of the Holocene.

Pseudomys praeconis was only sparsely represented in the Skull Cave deposit. However, Baynes (in Baynes *et al.* 1976) states that this is "typical of the species in the southern part of its range". It was also recorded from Turner Brook (Archer and Baynes 1972).

A notable absence from the faunal list for the excavation is *Thylacinus cynocephalus.* Several specimens have been recorded from various parts of Skull Cave in excavations made by other collectors (e.g. Howlett 1960). It has also been recorded from other caves in the Cape Leeuwin-Cape Naturaliste region (e.g. Merrilees 1968).

A comparison of the Skull Cave faunal assemblage was made with that of Devil's Lair, a cave about 14 km north of Skull Cave containing abundant mammal remains of late Pleistocene and early Holocene age ranging from about 35 000 yr to about 5 000 yr B. P. (Balme *et al.* 1978). It was found that five species (*B. lesueur, Petrogale* sp., *M. eugenii, M. irma,* and *Notomys* sp.) were present in the upper levels in Devil's Lair, but absent from Skull Cave, and two species (*Canis familiaris* and *Rattus tunneyi)* were present in the upper levels of Skull Cave but absent from Devil's Lair.

B. lesueur, Petrogale, M. eugenii and *Notomys* have been recorded from Yallingup Cave from sediment beneath "dripstone" layers. *Petrogale* and *M. eugenii* have also been found in Deepdene Cave in a deposit of which the lower level has been dated 19 400 ± 1 200 yr B. P. (Kigoshi, Suzuki and Fukatsu 1973). The former also occurred in Strongs Cave (Merrilees 1968), Giants Cave, Museum Cave and The Labyrinth (Merrilees 1979). To date, there have been no other confirmed fossil records of *Petrogale, M. eugenii* or *Notomys* in the Cape Leeuwin-Cape Naturaliste region.

There are several fossil records of *Macropus irma* both of known antiquity (e.g. from Mammoth Cave, Merrilees 1968) and of unknown antiquity. However, Baynes (in Baynes *et al.* 1976) notes that all show signs of chemical alteration or encrustation indicating considerable age. *Macropus eugenii* has been recorded from Yallingup Cave but these may be of considerable antiquity; there appear to be no fossil records of *M. eugenii* attributable to an age younger than early Holocene. Both species

have been recorded from the Cape Leeuwin-Cape Naturaliste region during historic time (Baynes *et al.* 1976).

Canis familiaris and *Rattus tunneyi* were present in the upper levels of Skull Cave but absent from Devil's Lair. Only a single canine of *Canis* was recovered from the excavations in Skull Cave, this being from a level 14-21 cm depth below the surface. Other specimens have been recorded from the surface of this cave and many others in this region.

Rattus tunneyi has been recorded only from the surface and the uppermost levels in Skull Cave; the oldest is from a level 21-28 cm below surface and which has been radiocarbon dated as 2 900 ± 80 yr B.P. (SUA 227). It has been recorded from the surface of deposits in Yallingup Cave, Brides Cave and Mammoth Cave and all of these specimens appear quite recent. *R. tunneyi* was also listed as occurring abundantly in a deposit in Cave 1 at Turner Brook by Archer and Baynes (1972) and they postulated a late invasion into the Cape Leeuwin-Cape Naturaliste region by this species. In view of the occurrences listed above, it is suggested the species arrived in the area of Skull Cave about 3 000 years ago, and presumably a little earlier in the northern part of this region. Baynes *et al.* (1976) add that this late arrival to the region may be due to it being able to "maintain large populations in pockets of vegetation among mobile sand dunes at beach edges". As suggested by Baynes, Merrilees and Porter for the other "non-forest" mammals in Devil's Lair, the route for the invasion of this region by *R. tunneyi* was probably via the coastal heath and scrubland to the west of the forest.

Discussion and conclusions

Although the faunal sample recovered from Trenches A and B was not large, some inferences about the history of some species during the Holocene can be made with supporting evidence from other localities in the Cape Leeuwin-Cape Naturaliste region. Balme *et al.* (1978) suggest that *Perameles, B. lesueur, Petrogale, P. albocinereus* and *Notomys*, all of which were absent from the region in historic time, became extinct locally at some time during the Holocene.

Notomys, and similarly *Perameles, P. albocinereus, P. praeconis* and *P. shortridgei*, are species not known to include forest in their habitat range (Baynes *et al.* 1976) and one would expect owls, and perhaps other predatory birds, to have collected all of these species if they were present in the heath and scrubland to the west of the forest. However, only the latter four are present in Skull Cave and the lack of *Notomys* probably reflects an absence of this species from the area during the Holocene. It is possible that the absence of *B. lesueur*, also a non-forest mammal, from the deposit may be due to its absence from the area since owls would probably take juveniles of an animal of this size, if not adults (cf. Smith 1977). Owls could also prey on young *Petrogale*, but its absence may be due to other factors.

The presence of species typical of forested areas (e.g. *Setonix brachyurus* and *Potorous tridactylus*) in nearly all levels of the deposit in Trenches A and B suggests the close proximity of forest to the cave during the whole period of deposition. Heinsohn (1968) noted that potoroos in Tasmania apparently did not leave the dense vegetation even to feed on the adjacent lush pasture. The presence of nearly complete skeletons of adult potoroos in Skull Cave could only represent the victims of the pit trap, and this would suggest that the cave was surrounded by forest and not by open vegetation during much of the Holocene. Most other species in the faunal sample include forest in their known habitats, and the species which are indicative of vegetation other than forest could have been brought into the cave by owls. Therefore, the absence of *Petrogale*, and possibly of *B. lesueur* also, may not necessarily reflect an absence from this region but merely indicate that these species did not venture into the forest surrounding the cave.

Balme *et al.* (1978) note a decline in the relative abundance of *B. lesueur, Petrogale* and *Notomys* from late Pleistocene to early Holocene time. It is possible that the range of these species did not extend as far south as Skull Cave or that *B. lesueur* and *Petrogale* did not enter the forest and their absence from Skull Cave may not represent their absence from this area. However, there is a lack of Holocene fossils of these species from other caves in the region which suggests a retraction northwards of their range before the Holocene.

Macropus irma and *Macropus eugenii*, two species which include forest in their habitat range, have not been found in Skull Cave. Balme *et al.* (1978) suggest that dwindling populations in late Pleistocene times may have retracted northwards during the Holocene. Baynes (in Baynes *et al.* 1976), postulates a re-invasion of the Devil's Lair district by *M. irma* after the first felling of the forests last century. He also lists the closest modern occurrence of *M. eugenii* to Devil's Lair as 30 km north at Ellenbrook. The absence of these species from Skull Cave, and the paucity of other records for most of the Holocene support the view of a retreat northwards of *M. eugenii* and *M. irma*, from at least the southern part of their late Pleistocene distribution, during the Holocene.

A forest mammal which has become extinct in this region, and probably elsewhere, during the Holocene is *Thylacinus cynocephalus*, although it has not been possible to date this extinction in the Cape Leeuwin-Cape Naturaliste region. Many specimens have been recovered from unsystematic excavations in Skull Cave, e.g. one recorded from a "shallow excavation" (69.9.11) and another (70.4.285) from approximately 0.6 m below the surface in the walls of an abandoned excavation in the "Thylacine Locality" (see Fig. 1). By reference to the dated sediments in Trenches A and B, it is suggested that *Thylacinus* survived in the area of Skull Cave well into the Holocene. It has

been suggested that the extinction of this species may be related to competition for similar food resources with the Dingo, which may have arrived in Australia early in the Holocene (Archer 1974).

Bowler (1976), Kendrick (1977) and Rognon and Williams (1977) have presented evidence for dry periods at various localities between about 7 000 and about 3 000 years ago. However, there appears to be no indication of changes in the faunal composition attributable to such climatic variation, although a larger sample would be necessary to confirm this. Present sea level was attained by about 6 000 years ago (Thom and Chappell 1975) and the extent of the heath and scrubland to the west of the forest presumably was relatively constant by this time.

During the Holocene, the forest mammal component of the fauna of the Cape Leeuwin-Cape Naturaliste region (with the exception of *Thylacinus cynocephalus* and possibly *B. penicillata*) appears to have remained consistent. However, of the heath- and scrub-dwelling species, *B. lesueur, Petrogale* and *Notomys* probably disappeared from this region during early Holocene time, and *Perameles and P. albocinereus* at some time after 3 000 years but before historic time. These local extinctions represent the culmination of trends begun in late Pleistocene times perhaps initially influenced by marine transgression, but it is suggested that climatic or human effects were the determinants during terminal Pleistocene and early Holocene times (Balme *et al.* 1978). It is possible that dwindling populations of *Perameles* and *Pseudomys albocinereus* became so depleted by about 3 000 years ago that they were no longer viable, despite a possible change in climate which may have been favourable to them.

Although there was a depletion of the fauna during the Holocene, two species entered the region at separate times. *Rattus tunneyi* invaded the coastal region and made its first appearance in the vicinity of Skull Cave about 3 000 years ago and may have persisted in the region until the arrival of European man (Baynes *et al.* 1976). *Canis familiaris* may have arrived in the region earlier in the Holocene, but at a time not yet known.

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